TORREYA

VOL. 45 MARCH 1945 NO. 1

Alternation of Generations and Classification With Special Reference to the Teaching of Elementary Botany*

HERBERT A. WAHL

The value of a scientific theory is usually directly proportional to the amount of thought and investigation which it stimulates. A theory loses its value when it becomes so generally accepted that the implications of the theory are considered as facts and stimulation of thought passes over to unquestioned acceptance of ideas as facts. Since what seems to be a fact in the light of certain evidence may lose its factual nature in the light of supplementary evidence, the periodic reexamination of established ideas is a constant scientific desideratum. This has been aptly expressed by Parkin and quoted by Douglas (1944) as follows: "It is well that from time to time there should be a stocktaking—a full appraisment of our botanical generalizations."

The various expressions of the phenomenon of Alternation of Generations as it occurs in the plant kingdom, while mostly in the realm of fact rather than of theory, embody various theoretical considerations some of which have become so well established as to be accepted as fact. Yet, in the light of accumulated evidence, they may now require additional appraisal.

It has long been recognized that the life cycle of vascular plants and bryophytes, as well as of many algae, consists of an alternation between two phases or generations each of which by a characteristic reproductive process initiates the other. These two growth phases or generations have constantly been referred to as the sporophytic phase or sporophyte and the gametophytic phase or gametophyte, since the former is spore-producing and the latter is gamete-producing. Further, it has been recognized since the time of Strasburger that the number of chromosomes in sporophytic nuclei is characteristically double that in gametophytic nuclei. The chromosome number is doubled by the fusion of gametes, the process that initiates the sporophytic phase, and halved by meiosis, the process which initiates the gametophytic phase.

Theories of alternation of generations deal chiefly with the origin and development of the phenomenon. One school of thought has maintained that the alternating generations are antithetic in their origin, that is, that the sporophytic generation arose by a gradual evolutionary development of the zygote following sexual reproduction and is a new structure not homologous in origin

* Contribution from the Department of Botany, The Pennsylvania State College, No. 146.

TORREYA for March (Vol. 45, 1-32) was issued April 20, 1945.

with the gametophyte, which was the original structure. The other school of thought has maintained that the two generations are parts of an original gametophytic generation, one part of which became spore-producing while the other part retained its gamete-producing function, thus giving rise to generations which are homologous in origin. The term homologous alternation of generations is used in two ways, however; in one sense to indicate the homologous origin of the generations and in another sense to indicate generations which are alike in appearance (isomorphic). It is not the purpose here to review the merits of the antithetic and homologous theories of alternation. Most of the references are to older literature and will be found in Svedelius (1927) as well as in current textbooks on plant morphology. The bearing of the present concept on the problem will be referred to in the latter part of this paper.

The phase of the phenomenon which has been widely accepted and which it is here considered may need revision is the application of the term "asexual" to the sporophytic generation and to its characteristic and "normal" method of reproduction, that is, by spores produced by the process of meiosis. This usage may depend, in the first place, upon one's definition of or understanding of what constitutes sexual and asexual reproduction. If the term sexual reproduction is to be used only to refer to the initiation of a new individual or generation of a life cycle by the fusion of cells, and if asexual reproduction is to be used to include all cases in which a new individual or a generation of a life cycle is initiated without such fusion, regardless of whether the same or another generation is thus initiated, then, by definition, the alternating generations in the life cycle of plants are sexually and asexually reproducing generations. Sexual and asexual reproduction have long been considered in the above manner, this is, the former as being characterized by a fusion of cells and the latter by a lack of fusion.

Selecting from the older literature we find the viewpoint that the sporophyte and gametophyte represent, respectively, asexual and sexual generations concisely expressed in an oft-quoted paper by Davis (1903). "The gametophyte is the sexual plant, developing the sexual cells or gametes. The sporophyte is asexual, producing spores." However, if we continue to follow the discussion in the same paper, we find expressed the state of knowledge which existed at that time concerning the chromosomes and their behavior. "If the question is asked why are the chromosomes so important and why should their number be so significant, no answer can be very satisfactory for our deep ignorance of the nucleus is exposed." "We do not know what the chromosome does——." "It will thus be seen that there can be no genetic relationship between the reduction phenomena of higher plants and animals. They are not found at the same points in the life history and there are also fundamental differences in the details of the process——." "——there is no reduction phenomena in plants at the time when sexual cells are formed——." "The

fact that the number of spores formed in each mother cell is four appears to have no important morphological significance. It has no connection with reduction phenomena which—take place before these divisions." Obviously, our knowledge of chromosome function and behavior has increased greatly since the above excerpts were first written. It seems equally obvious, however, that this knowledge has not been applied, or has been indifferently applied, in an interpretation of the relation of these phenomena to the sexual life cycle of plants.

It should by now be apparent that the process of sexual reproduction involves not only the fusion of gametes (syngamy) by which the zygote receives the sum of the chromosomal components of the two gametes, but that the process by which the chromosome number is reduced (meiosis) is an integral part of the sexual life cycle. In animals generally and in those plants (*Fucus*, diatoms, Siphonales) in which meiosis shortly precedes syngamy, this relationship is obvious. In most green algae and in other Thallophyta in which meiosis follows syngamy without the intervention of a growth phase or alternating generation, the relation should be equally obvious. In those plants in which a growth phase intervenes between syngamy and meiosis, that is, in which an alternation of generations occurs, the separation of syngamy and meiosis in point of time seems to have been instrumental in the frequent failure to associate the processes as integral parts of the sexual mechanism.

The difficulties which arise from the dissociation of the meiotic processes and syngamy and the association of meiosis with asexual reproduction have their beginning, as far as elementary teaching is concerned, in a consideration of the reproductive processes in the lower plant groups. In many algae, vegetative (asexual) reproductive cells such as zoospores, aplanospores, etc., are produced by the haploid plant body while the same plant body produces gametes. Following the fusion of gametes, the next reproductive process in the life cycle of many common algae is the meiotic division of the nucleus of the zygote, a process which results in the production of four spores. Since asexual reproduction has consistently been considered as including all reproductive processes not directly initiated by a fusion of cells and since it refers especially to the production of spores, the tendency here is purposely or passively to homologize the vegetatively-produced spores with the spores produced as a result of meiosis. The vegetative production of spores is exactly comparable as a reproductive method to the production of gemmae by liverworts and mosses and to the production of gemmae, bulblets and the host of other vegetative reproductive devices by vascular plants. The reproductive methods are entirely comparable regardless of the fact that we are here comparing processes of the gametophyte with those of the sporophyte; they all consist of the rejuvenation of an individual by the initiation of growth from some more or less specialized portion of the vegetative plant body. In some algae in which an alternation of generations occurs (e.g. *Cladophora*)

vegetative spores are produced by both generations, those produced by the haploid generation producing haploid plants and those produced by the diploid generation producing diploid plants.

Of an entirely different nature are those cells (meiospores) produced by vascular and non-vascular plants as a result of meiosis. These are not vegetatively produced; they are produced only by organisms having sexual reproduction and their production represents a continuation of the sexual process. They do not produce the generation from which they originated but having been formed as a result of a reproductive process in a diploid generation, the product of their growth is a haploid generation. In some cases (diatoms, Siphonales) they may be the only haploid cells; they are, functionally, gametes. They are fundamentally different from vegetative spores (zoospores, aplanospores, etc.); in no sense are the two kinds of so-called spores homologous. How then can the term asexual reproduction be used to refer to reproduction by these entirely different methods?

That it is so used is evident from the treatments in most of the numerous current textbooks covering the field of Elementary Botany. In almost all of these that the author has examined, no clear distinction is made between the actual nature of vegetative spores and meiospores. The production of both and the initiation of a new individual by their growth is generally included under the term asexual reproduction. These two kinds of reproductive structures, one strictly vegetative and the other associated with sexual reproduction are homologized either directly or by inference. In most cases the gametophyte is described as a sexual generation because it produces gametes and the sporophyte as an asexual generation because it produces spores and the same terminology is used to describe vegetative spores and meiospores. In one of the more recent texts (Smith et al., 1942), the term asexual reproduction is entirely eliminated but even here the reader is led to infer that the spores produced by meiosis are in the same category as the vegetatively-produced spores of green algae, since no effort is made to distinguish between them.

Although the author has not attempted to be exhaustive in his review of the numerous current elementary textbooks, a majority of those published in the United States have been examined. In only three of these is sexual reproduction used in the sense of referring to the complete reproductive life cycle. In the relatively brief and elementary textbook by Chamberlain (1930) "gametic reproduction" is considered as including the complete reproductive process, consisting of the fusion of gametes and the consequent production of the original plant by meiospores (Fig. 147). Even here, however, the same term, zoospore, is used to denote both vegetatively produced spores and meiospores so that confusion between the fundamentally different reproductive processes by which they are produced is made easy in the mind of the student.

In a more recent text (Weatherwax, 1942), one that is also intended for use in a shorter course, the author considers the production of meiospores as part of sexual reproduction. "The complete sexual life cycle consists of two generations, the gametophyte and the sporophyte, which follow each other in alternate sequence." (p. 196.)

It is refreshing to note that this viewpoint which considers a life cycle involving an alternation between a gametophytic phase and a sporophytic phase as a sexual life cycle is at least partially maintained in one of the more extensive modern elementary texts (Transeau, Sampson and Tiffany, 1940). In discussing reproduction in *Ulothrix* the authors state: "The special method of vegetative multiplication by means of either motile or non-motile spores which are formed without a previous union of gametes is often termed *asexual reproduction*. The related series of processes including the formation of gametes, their subsequent union, and the development of the resulting zygote into motile spores from which new filaments develop are referred to as the sexual reproduction of the algae." The life cycle of flowering plants is also considered a sexual life cycle and by inference the sporophyte is as much a sexual individual are are the gametophytes. It is a bit disconcerting, however, to find under the discussion of liverworts the heading "The sporophyte and asexual reproduction" leading to the inference that here the production of meiospores is not part of sexual reproduction and that the sporophyte is an asexual generation.

The above mentioned cases constitute the exception. From a consideration of other books, it is apparent that the student is in most cases introduced to the idea that following sexual reproduction (fusion of gametes, or syngamy) an asexual reproductive process (production of spores by meiosis) occurs. This must be expanded in the higher plants to include the idea of alternating sexual and asexual generations with their concomitant methods of sexual and asexual reproduction. The elaboration of the idea of alternating sexual and asexual reproductive methods by Coulter (1914) has probably been of greater importance in perpetuating this concept than any other work.

Several disadvantages of this viewpoint may here be pointed out. In the first place, the concept of a life cycle involving an alternation of sexual and asexual reproduction and sexual and asexual generations is inherently more difficult for the beginner to grasp than the same series of events explained in terms of a continuous process as a sexual life cycle. Let it not be thought, however, that the present author would condone any presentation which merely substitutes simplicity for correctness. The greater simplicity of considering the life cycle a sexual cycle has been demonstrated in class work. The assumption that the viewpoint is correct is based, of course, not on new facts but on an evaluation of accumulated ideas.

In the second place, the consideration of the sporophyte as an asexual generation and the production of spores by meiosis as an asexual process leads

naturally to a comparison and homologizing of vegetatively-produced spores of algae with meiospores, though the two are fundamentally and entirely unlike in their significance in the reproductive life cycle. This has been referred to earlier in the present paper.

Thirdly, the consideration of reproduction by spores produced by meiosis as a strictly asexual process in contrast to sexual reproduction by the fusion of gametes has tended to dissociate the two cytogically important processes in the life cycle;—syngamy and meiosis. Too often in elementary (and advanced) texts the reduction in chromosome number which occurs at meiosis is considered as occurring during *a division* which is *contrasted with an ordinary cell division* (mitosis). It is generally recognized that the reduction in chromosome number occurs during a series of *two* divisions; that the term, *a reduction division,* is decidedly a misnomer. It is well known, even by those who are responsible for statements in textbooks such as "—in reduction division—the chromosomes do not split at all—", that the chromosomes *do* split during the first meiotic division. But this is done in an attempt to contrast "reduction division" with mitosis, since "—in ordinary cell division the chromosomes split longitudinally—." Now the reduction in chromosome number is not a process to be contrasted with mitosis, since it itself may be considered as consisting of two mitoses (Sharp, 1934, Chap. 16), but is a process to be contrasted with syngamy. Meiosis is not simply a type of cell division but represents the culmination of the sexual process which is initiated by the fusion of gametes. The process of syngamy introduces the two sets of chromosomes into one nucleus. The final association of the chromosomes during which there occurs not only an intimate association (synapsis) but even an interchange of parts (chiasmata formation; crossing over) takes place during meiosis, the culminating feature of sexual reproduction. The sporophytic generation is an interlude in the sexual process. The sporophyte is a sexual generation. The meiotic production of spores and the growth of a new individual from each is part of the process of sexual reproduction.

In advanced texts dealing with the groups of plants, the viewpoints are variable. Fritsch (1935) distinguishes between the significance of zoospores from the haploid plant and those from the zygote, since in discussing the life cycles of Algae he says, "—in addition to reproducing by sexual means it (the gametophyte) may also exhibit abundant asexual reproduction. This latter is, however, actually an accesory means of reproduction and, in relation to the general course of the life cycle, has not the same significance as the formation of asexual swarmers or other reproductive cells from the zygote which ensues after the occurrence of meiosis." (p. 51). The distinction is not clearly followed, however, since the production of asexual spores (zoospores, aplanospores, etc.) by the gametophyte and the production of spores from the zygote by meiosis are both considered under the discussion of asexual reproduction and

no mention is made of the latter in what is here considered their proper relation, that is, as part of the sexual process. The sporophyte is considered an asexual generation and the production of meiospores is considered an asexual process. In fact, in a previous paragraph (p. 41) the statement is made that "Of a comparable nature to aplanospores are the endospores formed in certain Myxophyceae and the tetraspores of Rhodophyceae and Dictyotales." This may be meant to refer only to their method of formation, however, and not to their significance in the life cycle.

Although Fritsch's book is not intended for use in elementary courses in general botany, the above quotations serve to emphasize the difficulties that arise with beginning students when a life cycle is considered as consisting of an alternation between a sexual and an asexual phase in which the sexual phase may also reproduce asexually, and in which the asexual phase may also reproduce by other asexual or vegetative methods which have not the same significance as its "normal" method of reproduction. How much simpler, and more correct, to consider the sexual life cycle as including syngamy and meiosis, with the interpolation of growth phases, either or both of which may have vegetative (asexual) methods of reproduction.

Smith (1933, 1938a), in his treatments of the Algae, generally considers the meiotic production of spores under the heading of asexual reproduction, except where meiosis shortly precedes syngamy, as in *Fucus,* in which case it is part of the sexual process. He does, however, distinguish, in some brown algae, between meiospores and vegetative spores, designating the latter as "neutral" spores since they produce the same type of plant from which they originate. In the case of *Fucus,* it seems at least as logical to consider the plant a gametophyte in which meiosis has been delayed until the production of gametes, the sporophytic generation having been eliminated or never produced, as to consider a plant that produces cells which function as gametes a sporophyte because the cells of the plant are diploid.

In his treatment of the bryophytes and pteridophytes, Smith (1938b) definitely considers the gametophyte a sexual generation and the sporophyte an asexual generation, although he describes the gametophytes as also reproducing asexually by gemmae and by other vegetative methods. The same viewpoint is expressed by Campbell (1918) in his "Mosses and Ferns."

Tilden (1935), on the other hand, considers the alternation of generations as an alternation between sexual generations. "*Sexual reproduction,* in the plant and animal kingdom includes, or has to do with, the entire normal life cycle, consisting of a morphological or cytological alternation of haploid and diploid generations. The sporophyte is as much a sexual organism as is the gametophyte, since it carries in its body the sex-bearing chromosomes" (p. 236). She restricts the use of the term spore to reproductive cells which are the products of meiosis, and this process is considered part of sexual reproduction. "Sexual

reproductive bodies include gametes and spores." For the vegetative (asexual) "spores" of algae (zoospores, aplanospores, etc.) she uses the term *gonidia.* These may be either motile (planogonidia) or non-motile (aplanogonidia).

In discussions of alternation of generations other than in textbooks, the viewpoint that the sporophyte should be considered a sexual generation has been maintained by Chamberlain (1905) and by Svedelius (1927). The latter, after referring particularly to the life cycle of *Fucus* makes the following statement: "From this it is evident how misleading it is to characterize the alternation of generations as an alternation between sexual and sexless generations. On the contrary, it is a characteristic feature of this evolutionary process that in the course of the increasing disparity of the generations in the direction of the dominance of the sporophyte, sexuality passes over more and more to the originally 'sexless' generation." To this it may be added that the "sexless" generation need no longer be considered as having been even originally sexless since, as Svedelius himself states in a later paragraph, "In a certain measure reduction is to be regarded as the final act and the goal of fertilization." It is becoming ever more apparent that reduction (meiosis) and fertilization (syngamy) are actually and inseparably both involved in the ordinary process of sexual reproduction, together with the generations which precede and initiate them.

In the voluminous literature referring to sex determination in plants, the sporophytic generation is regularly referred to as exhibiting features of sexuality. Indeed the very term "sex determination" as it is ordinarily applied to angiosperms, would otherwise be meaningless. "Any genetic analysis of sex in angiosperms must deal almost exclusively with characters of the so-called asexual generation, since those of the much-reduced haploid 'sexual' generation have yet afforded little material for genetic study. To speak of sexual characters in an asexual generation is paradoxical; but the paradox inheres in the terminology, not in the facts" (Allen, 1932, pp. 97-98). This viewpoint is accepted by Loehwing (1938).

Thus occurs a paradox in scientific terminology whereby a term in general use admittedly is not even intended to mean what its definition implies. For those who have been "brought up" on such usage to continue to use it while admitting its incorrectness may be in slight degree justifiable; to continue to "bring up" succeeding generations of botanists on an admittedly incorrect viewpoint because of the unwillingness of textbook writers (and I suppose of many teachers) to incorporate new ideas into their teaching is not consistent with the best scientific practice.

The question of terminolgy then arises in connection with the consideration of the sporophyte as a sexual generation. Sharp (1925) has discussed terms to be used in implying sexuality to the sporophyte and it may be useful to have a set of terms separate from those applied to the gametophyte. We are

here concerned, however, only with those reproductive terms constantly used in an elementary presentation. We have already called attention to the confusion that may result when the term asexual reproduction is used in connection with vegetative reproductive processes and with the production of meiospores. Since the latter is part of sexual reproduction, since the term vegetative reproduction adequately describes the former and since asexual reproduction has been used to denote entirely different processes, it would seem best to discontinue use of the term asexual reproduction entirely. This, as before mentioned, has been done in one recent text. Tilden (1935) uses the term *spore* only for meiospores and the term *gonidium* for vegetatively produced spores. It seems more expedient to the author to continue the use of the term spore for both of these categories, simply recognizing that meiospores (including ascospores and basidiospores) are sexual spores while other kinds of spores are vegetatively produced. Spores, then, are usually one-celled reproductive bodies which produce new plants by direct growth, in contrast to gametes which are one-celled reproductive bodies which fuse together. For the purpose of teaching Elementary Botany it is unfortunate that there exist in the plant kingdom such a multiplicity of kinds of spores. The facts make necessary the application of numerous prefixes to describe certain types of spores such as zoospores, conidiospores, uredospores, meiospores, etc., etc. The problem is not simplified by failing to recognize that some of these are vegetatively produced while others are involved in the sexual reproductive processes.

We may now comment briefly concerning the bearing of the ideas presented in this paper on the relative merits of the antithetic and homologous theories of alternation of generations. Fritsch has been one of the leading proponents of the idea that the origin of the alternating generations, at least as they occur in members of the Pteridophyta, is to be sought in the type of algal plant body which occurs in certain members of the Chaetophorales of the Green Algae. Members of this group exhibit the heterotrichous type of plant body which consists of a prostrate creeping system, often more or less pseudoparenchymatous, and a more or less upright system of usually branching filaments. In some cases (e.g., *Trentepholia*) zoospore production is confined to the upright system and gamete production to the prostrate system.

According to Fritsch (1916, p. 240) this condition provides "all the necessary indications for the gradual differentiation of two alternating generations, of which one bears the asexual organs on the upright system, the other bears the sexual organs on the creeping base. Disappearance of the base in the former, and of the upright system in the latter—will give two different generations, resembling those of the Archegoniatae in all respects." This is incidentally referred to again in a later paper (1920, p. 170). "An alternation between sexual and asexual phases must have come about as soon as the reduc-

tion-division became associated with spore-formation—." He then refers to the "relegation of the reduction-division to the time of spore formation." Herein is expressed a fallacy to which we readily fall heir when the alternating gametophytic and sporophytic generations are considered as being respectively sexual and asexual; a fallacy which is inherent in any theory of the homologous origin of the alternating generations. This line of reasoning directly and purposefully homologizes meiospores, which are always and only produced during the series of processes involved in sexual reproduction, with the vegetatively produced spores of algae. It postulates an origin of the meiotic processes in connection with the vegetative production of spores rather than confining it to the only conceivable place in which it could possibly have a function, namely, as a result of the process in which the chromosome number is doubled. Meiospores can have no homologous identity with vegetative spores. The latter are considered by many to be homologous with gametes, since the usual theory of the origin of sexual reproduction considers that gametes are modified vegetative spores. It is altogether logical that the cells produced as a result of the meiotic processes following sexual fusion in various primitive plants should simulate in appearance the vegetative spores produced by that particular plant, since new genes for the production of somatic characters would not necessarily be produced at the same time that sexual reproduction had its origin. But to consider these cells as being homologous in origin would be comparable to considering as homologous the leaves of mosses and of lycopods, or root hairs of vascular plants and rhizoids of fern prothallia. From the viewpoint of the present paper, therefore, the alternating generations in a sexual life cycle such as occur in all plants above the Thallophyta, and in many Thallophyta, could not be considered as having had a homologous origin.

This paper has thus far attempted to show that the usual textbook presentation of the "asexual" nature of the sporophyte should be corrected in favor of considering the alternating generations in the life cycle of plants as parts of the sexual life cycle. Although both viewpoints are to be found in current texts, the former has the weight of numbers and the sanction of long continued usage. Of even greater uniformity both from the standpoint of unanimity of presentation and of admitted incorrectness is that part of most botanical texts which serves, or should serve, the dual purposes of presenting the groups of plants in an orderly sequence and of indicating the supposed relationships between the groups,—the system of classification. The time-honored system of Thallophyta, Bryophyta, Pteridophyta and Spermatophyta serves the first of these purposes but lacks woefully in serving the second, especially as between the groups included in the last two divisions. It has been expressed as a truism that no morphologist considers the ferns, lycopods and horsetails closely related. Yet, in the great majority of elementary texts the lycopods and horsetails are "the allies of the ferns." The fact that this system

"has been so generally adopted" (in the past) does not argue in its favor since it is well recognized that it does not express the present state of knowledge regarding plant relationships.

Systems of classification reflecting modern ideas of relationships in the entire plant kingdom have been prepared among others by Copeland (1938), Barkley (1939), and Tippo (1942). The systems here referred to certainly are not to be considered "new" at this time since they draw on a wealth of morphological knowledge, most of which has been available for two decades or more. Neither are they only the opinions of their respective authors, since they represent the accumulated efforts and opinions of many specialists in various groups. Herein lies one of their best recommendations. Yet at the present time hardly an elementary textbook even mentions these ideas without apologies! Where would genetics or plant physiology be if similar accumulations of ideas in these fields were studiously withheld until they had mellowed for a quarter of a century?

Why do elementary texts shy away from the presentation of such accumulated knowledge? The usual claim that the older system is easier is only partially true. One system of classification is not easier than another for a beginner. It is only the one who has been used to the older system who would have difficulty in making a change. "Easier," then, can only mean that it is easier for the teacher, not that it is easier for the student.

This leads naturally to the conclusion that textbooks are written for the convenience of the teacher rather than for the information of the student;—that pedogogy is for the pedagog rather than for the learner. Such a conclusion, is, of course, not valid for the majority of the subject matter in most textbooks available at the present time. But what other reason could be assumed when an author, for example, relegates an admittedly "modern" system of classification to an appendix while using an admittedly outmoded system in the body of the text? Or when an author admits that "a better classification" separates plants into groups other than those with which he has tried to make the student familiar?

It seems apparent that modern textbooks of elementary botany have been "leaning over backward" in an effort to maintain a conservative viewpoint in the field generally designated as Comparative Morphology. Although there may be room for divergence of opinion as to the relative emphasis to be placed on the various materials presented to beginning students, especially in the briefer courses, there seems to be no tendency to exclude a consideration of the comparative structural and reproductive features of the 15 to 18 groups (usually classes) of plants ordinarily considered as constituting a fair representation of the plant kingdom. This usually (but not necessarily) involves classification and life cycles. If a system of classification is to be presented, why not let it reflect modern ideas of relationships? If life cycles are thought desirable, a con-

sideration of the complete life cycle as a sexual process may focus attention more forcefully on the genetical aspects of chromosome behavior and may serve to modify their "prolonged and prayerful consideration" in the direction of greater simplicity and proper scientific evaluation.

Department of Botany, The Pennsylvania State College
State College, Pennsylvania

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